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Photo-physiological responses and thermal tolerance of regionally endemic/rare and morphologically different corals of the Western Indian Ocean

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Abstract. *Munbodhe V, Jeetun S, Ricot M, Jogee S, Kaullysing D, Bhagooli R. 2023. Photo-physiological responses and thermal tolerance of regionally endemic/rare and morphologically different corals of the Western Indian Ocean. Indo Pac J Ocean Life 7: 100-107.* Intensification in climatic variations is causing major alteration in ecosystem functionalities and an overall decline in reef biodiversity. Underlying the ongoing cumulative threats and the vulnerability to biodiversity loss in the reefs, this study aims to determine the photo-physiological response and the thermal tolerances of the morphologically different coral species namely, *Porites lutea, Porites cylindrica, Acropora hyacinthus, Galaxea fascicularis, Seriatopora hystrix* including the two regionally endemics of the Western Indian Ocean, *Acropora branchi* and *Pocillopora indiania*. Coral fragments from three colonies per species were collected from the south and southeast of Mauritius Island and treated at 27°C, 30°C and 32°C for 19 hours. Using a diving Pulse-Amplitude-Modulated (D-PAM) fluorometer, the effective quantum yield at photosystem II (ΦPSII) was recorded from the coral fragments initially and following 3, 6 and 19 hours of treatment. This experiment determined the thermal threshold of the understudied *A. branchi* and *P. indiania,* and detected the unexpectedly enhanced thermal tolerance of *S. hystrix* and *G. fascicularis*. Overall, it provides a preliminary insight into potential thermal stress tolerance in some Mauritius corals and has shown that these corals might have strategized to enhance their thermo-resilience while others are still struggling to withstand such stresses. These findings on the thermal resilience of regionally endemic/rare and morphologically different coral species are essential for further reef conservation efforts and the selection of coral species for reef restoration.

Keywords: Coral morphology, photo-physiological response, regionally endemic corals, thermal stress, thermal tolerance

INTRODUCTION

Compounding effects from both climatic variabilities and massive disturbances arising from the ever-increasing anthropogenic activities have resulted in immense loss of the 3-dimensional structure of the reefs (Elliott et al. 2018; Richardson et al. 2018). Warm sea surface temperatures have seriously damaged and killed up to 16% of the world's coral reefs (Steffen et al. 2009) and under the current warming scenario (Klepac et al. 2022), coral reefs are expected to undergo further major benthic transformation (van Hooidonk et al. 2015). Australia's Great Barrier Reef has already experienced this phenomenon eight times, causing mass bleaching since 1979 with the most widespread events occurring in 1998 and 2002 whereby more than 50% of reefs bleached (Steffen 2009). Likewise in the Caribbean, about 80% of the reefs was affected in 2005, while since 2014, three major bleaching events were recorded, with 2014 in the Northern tropical Pacific, 2015/16 over the tropical oceans (Lough et al. 2018) and 2017/18 in the Western Indian Ocean (WIO) (Obura et al. 2019).

To understand the mechanism of coral bleaching, Pulse-Amplitude-Modulated (PAM) fluorometry has been used to measure changes in photosynthetic activities and the response of corals to increasing sea surface temperatures as well as to changes in light intensity with increasing depth (Bhagooli and Hidaka 2003; Hoogenboom et al. 2012; Louis et al. 2016; Bhagooli et al. 2021a). The rate of bleaching varied significantly in different coral morphs with increasing degrees of temperature, for example, in *Acropora selago*, the expulsion mean number of degraded cells from corals increased from 36 degraded cells at 27°C to 60 degraded cells at 30°C and 54 degraded cells at 27°C to 75 degraded cells at 30°C in *Acropora muricata* (Fujise et al. 2014). Furthermore, photo-physiologically, not all corals react in the same manner (Bhagooli and Hidaka 2003; Fitt et al. 2009; Tilstra et al. 2017; McWilliam et al. 2018; Serrano et al. 2018; Mattan-Moorgawa et al. 2020) to severe and frequent prolonged marine heating (Hobday et al. 2016; Stillman 2019). Some suggest that corals from highly diverse coral reefs are more thermotolerant with relatively high productivity (McWilliam et al. 2018). Others infer that varying size and shape of the corals may respond differently (van Woesik et al. 2011) whereas corals exposed to vast thermal variabilities tend to show more thermal resistance than those from thermally stable environment (Louis et al. 2016, 2020; Safaie et al. 2018; McClanahan and Muthiga 2020; Voolstra et al. 2020).

Furthermore, it has been reported that local factors such as over-fishing, nutrient enrichments (Serrano et al. 2018), and sedimentation (Shantz and Burkepile 2014) contributes significantly to algal over-growth, thereby compromising the resilience of corals by making them more vulnerable to thermal bleaching (Holbrook et al. 2018). Under certain conditions, Baird and Marshall (2002) successfully provided evidence that the corals of the same genera exhibited different reaction to the thermal stress whereby, *Acropora millepora* was not only more resistant than *A. hyacinthus* but also remarked that certain colonies of the same *Acropora* species survived the entire bleaching event while others died. Moreover, despite elevated temperature, *Stylophora pistillata* and *Galaxea fascicularis* could tolerate thermal stress under favorable food conditions and thus sustain symbiotic photosynthetic activities implying thermal adaptability (Borell and Bischof 2008).

Yet, lethal coral bleaching has been increasing in frequency, severity, and geographic scope over the past decades, and thus it is anticipated that this trend will continue (Grottoli et al. 2014; Hughes et al. 2017) which therefore increases the fragility of reefs (Goldberg and Wilkinson 2004) leading to biodiversity loss (McClanahan et al. 2021) and rapid community structural changes (Tebbett et al. 2023). To date studies on corals of Mauritius have looked at bleaching and mortality of corals under thermal stress (Bhagooli and Taleb-Hossenkhan 2012; Bhagooli and Sheppard 2012; Bhagooli and Kaullysing 2019; Bhagooli et al. 2021b,c; Fai et al. 2023; Jeetun et al. 2023; Ricot et al. 2023). However, rare and endemic corals' responses to thermal stress in the Mauritian waters is almost uncharted. Underlying the ongoing cumulative threats and the vulnerability to biodiversity loss, this study examines whether the degree of thermal stresses vary with respect to coral growth-forms, branching, tabular, massive and sub-massive corals and assess the thermal threshold of the under-studied regionally endemic coral species. Overall, it aims to elucidate impact of the increasing severity of thermal stresses and determine the photo-physiological responses and the thermal tolerances of the morphologically different coral species including the two regionally endemics of the WIO.

MATERIALS AND METHODS

Study area

The Republic of Mauritius is an oceanic state in the Western Indian Ocean which has several outer islands harbouring highly diverse corals and reef fishes (Obura 2012). Mauritius, the main island of the Republic of Mauritius, has an overall lagoon area (shallow waters) of 243km^2 enclosed by about 150 km of fringing reefs. The reefs are distinctly broken by natural breaks giving rise to a series of lagoons that defines the geomorphological characteristics such as depths, current pattern and stretches from the shore (Daby 2006). The depth of the lagoons varies between <1 to 3m from near shore extending a few kilometres to the reef with some exceptions in the southeast region where channels of < 30m deep mainly associated with rivers or underground springs separate the reef from the shore (Elliott et al. 2018). Serious concerns on the decadal increase in atmospheric temperature at the rate of 0.5°C per decade were raised following the metadata analysis which had shown that weather condition in Mauritius is experiencing a mean highest temperature of 31°C in summer and mean lowest temperature of 14°C in winter (Boojhawon et al. 2010). In addition, the reefs of Mauritius are also exposed to ongoing coastal clearing and intense near-coast and inland urbanization (Elliott et al. 2018), making them more vulnerable to unprecedented risks of local extinctions (Obura et al. 2017; McClanahan and Muthiga 2020).

Subsequently, this study was designed to assess the thermal tolerance of *Acropora branchi* and *Pocillopora indiania*, the regionally endemic corals along with *Acropora hyacinthus*, *Porites lutea* and *Porites cylindrica* and *Seriatopora hystrix*. These coral specimens were collected in the form of 2-2.5cm^2 fragments from different coral colonies of the same species from the backreef and mid-lagoon of Riviere des Galets from the South of the Island, whereas *S. hystrix* fragments which are among the rare coral species were collected from Bambous Virieux, mid-lagoon which is situated in the eastern part of Mauritius (Figure 1). Both lagoons are continuously exposed to the South East Trade winds with a water depth varying from 0.75m to 1.5m at the high tide. The *A. branchi, A. hyacinthus, P. indiania, P. lutea* and *P. cylindrica* were relatively abundant at Riviere des Galets, 20° 30.706'S; 57° 27.903'E while *S. hystrix* was found in the eastern part of the island at Bambous Virieux, 20° 20.925'S; 57° 46.057'E.

Thermal stress experiment

Based on the occurrences, in February 2022 coral fragments were collected from the two selected sites and were brought in buckets under dim light to Environmental Sciences Wet Laboratory at the University of Mauritius. The fragmented samples were transferred to 2000L tanks equipped with air pumps for at least two hours of settling before the thermal stress experiment. Nine coral fragments (n=9) were used during the experiment, whereby three coral fragments per coral colony of the same species were placed in three different aquaria of the same treatment (triplicates), whereby nine sets of photophysiological readings from each treatment were obtained. The nine aquaria (400-500L) were equipped with air pumps and thermostats to maintain the dissolved oxygen level to an optimal level and maintain the water temperature to the desired experimental level. The initial temperature in all 9 tanks was about 27°C (normal SST) and salinity at ~35 ppt. Three aquaria (3x Tank 1) were used as Control while the 6 others were used for bleaching with temperature gradually raised to 30°C (thermal threshold) in aquaria Experimental Tank 2 and 32°C (induced stress) in aquaria Experimental Tank 3 (Figure 2).

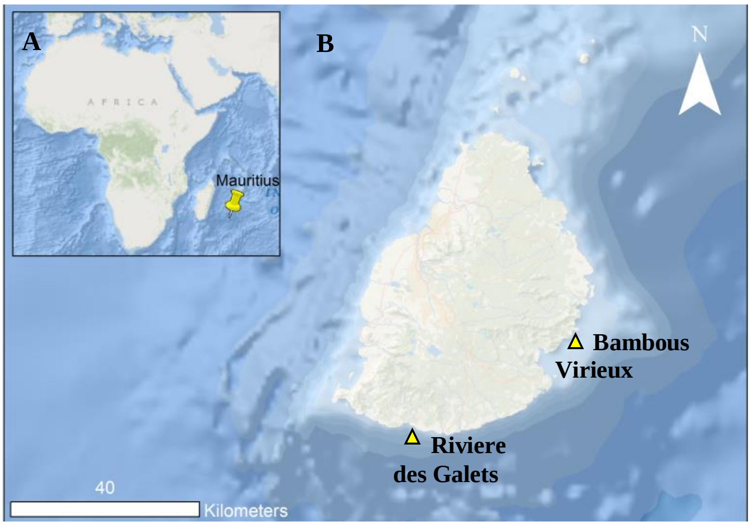

Figure 1. A. Location of Mauritius in WIO indicated by yellow pin, B. Sites where coral samples were collected; Riviere des Galets; bleaching surveys were carried out in January and April 2019 and coral fragments from six coral species were collected for thermal stress experiment while only fragments from one species from Bambous Virieux was collected i.e., *Seriatopora hystrix* which is relatively rare and occurrence is site specific

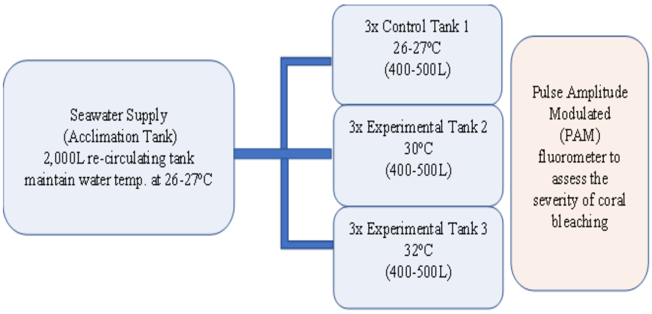

Figure 2. Experimental design for thermal stress using three different treatment tanks at 27°C, 30°C and 32°C with each treatment having three experimental tanks (triplicate) and each experimental tank having three coral fragments of the same species (3 coral fragments x 3 experimental tanks per treatment, n=9 per coral species)

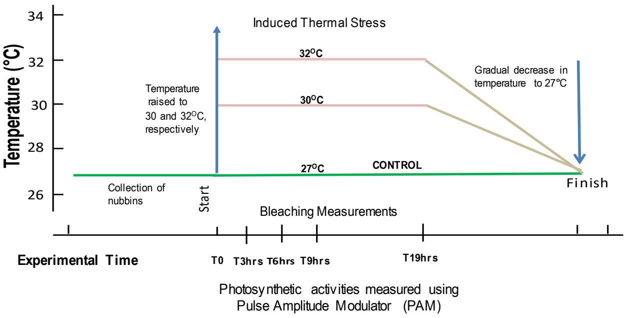

Figure 3. Conceptual diagram showing the different steps involved in the thermal stress experiment from the collection of coral fragments to exposure to different temperatures and the timely measurement of photosynthetic activities

Prior to placing the coral fragments in their respective treatment tank, photo-physiological data was recorded at the beginning of the experiment, i.e., $Time_{initial}$ or $Time_{zero}$ was collected prior to placement of the coral fragments in each water tank using the Pulse-Amplitude-Modulated (PAM) Fluorometry (Bhagooli and Hidaka 2003; Bhagooli et al. 2021a). Same exercise was repeated at three hours, six hours and 19 hours as demonstrated by the conceptual diagram (Figure 3).

Data analysis

MS Excel and R-Statistical software, R-4.2.2 were used to compile and analyse the effective quantum yield, Φ_{PSII}. The bar-plots were used to display thermal stresses, Φ_{PSII} of each coral species following persistent exposure to varying temperatures under experimental conditions. The percentage reduction in the photosynthetic response (relative to initial) was derived from the mean effective quantum yield of each coral species to that of initial mean Φ_{PSII} for every treatment. As the data on the Φ_{PSII} was not normally distributed (Shapiro-Wilk Test for normality), non-parametric statistical analysis was performed to assess the impact of elevated temperature on the Φ_{PSII}. Kruskal-Wallis Test shed light on the variation in photosynthetic activities combined for all coral species with respect to mean effective quantum yield (Φ_{PSII}) at the different treatments over time, while the Dunn's (1964) Kruskal-Wallis Post-hoc test allowed multiple comparison of the mean effective quantum yield (Φ_{PSII}) at different treatments after 3 hours, 6 hours and 19 hours of thermal stress experiment.

RESULTS AND DISCUSSION

Thermal stress experiment

The thermal stress experiment showed that *A. branchi* (Φ_{PSII} = 0.007±0.001 at 30°C and ΦPSII = 0.006±0.001 at 32°C), *A. hyacinthus* (Φ_{PSII} = 0.11±0.04 at 30°C and Φ_{PSII} = 0.00 at 32°C) and *P. cylindrica* (Φ_{PSII} = 0.009±0.003 at 30°C and Φ_{PSII} = 0.02±0.03 at 32°C) were photo-physiologically inactive after 19hrs exposure to 30°C and

32°C, respectively. The coral fragments of *A. branchi*, *A. hyacinthus* and *P. cylindrica* were completely bleached while, after persistent exposure, *P. lutea* (Φ_{PSII} = 0.476±0.008 at 30°C and Φ_{PSII} = 0.357±0.007 at 32°C), *G. fascicularis* (Φ_{PSII} = 0.0.463±0.067 at 30°C and Φ_{PSII} = 0.164±0.007 at 32°C and *S. hystrix*, (Φ_{PSII} = 0.677±0.003 at 30°C and Φ_{PSII} = 0.185±0.081 at 32°C) exhibited relatively higher photosynthetic activities. Conversely, *P. indiania* was photo-physiologically active after 19hrs of persistent exposure to 30°C, (Φ_{PSII} = 0656±0.05 at 30°C) with tissue blushing and paling/partial bleaching which eventually could not resist higher thermal stress of 32°C at 19hrs (Φ_{PSII} = 0.002±0.002 at 32°C).

Overall, the photosynthetic activities remained at maximum within the first 3 hours of the experiment which then gradually varied significantly at 6 hours and at 19 hours ($p<0.001$, Table 1). However, at 6 hours, no differences in photo-physiological activities was observed in coral fragments exposed at temperatures 27°C and 30°C ($p=0.266$) as compared to 27°C and 32°C and 30°C and 32°C which differed significantly ($p<0.0001$, Table 2). Relatively only about 10% drop in the effective quantum yield in corals was recorded during the first 6-hrs at 30°C which intensified after persistent exposure (19 hours) whereby the photosynthetic activities of *A. branchi*, *A. hyacinthus*, and *P. cylindrica* were ceased completely while *P. indiania*, maintained 80% - 90% of its photo-physiological activities both at 30°C/19 hours and 32°C/6 hours whereas complete bleaching was observed at 32°C/19 hours as depicted in the bar-plots (Figure 4). Most of the corals exhibited 60% (relative to initial) of photo-physiological response to 32°C within the first 6 hours of the experiment. However, only *P. lutea, G. fascicularis* and *S. hystrix* were capable to maintain photo-physiological response to persistent higher temperature of 32°C for 19 hours at a rate of 47%, 22% and 23%, respectively (Figure 5), while the rest of the coral fragments were completely bleached and smothered.

Table 1. Kruskal-Wallis Test: Variation in photosynthetic activities combined for all coral species with respect to mean effective quantum yield (Φ_{PSII}) at the different treatments over time; p<0.01, sig. *, p<0.001, sig. **, p<0.0001, sig. ***

Experiment duration	Chi-squared	d.f.	p-value
3 hours exposure	7.249	2	0.026
6 hours exposure	30.282	2	<0.0001
19 hours exposure	36.696	2	<0.0001

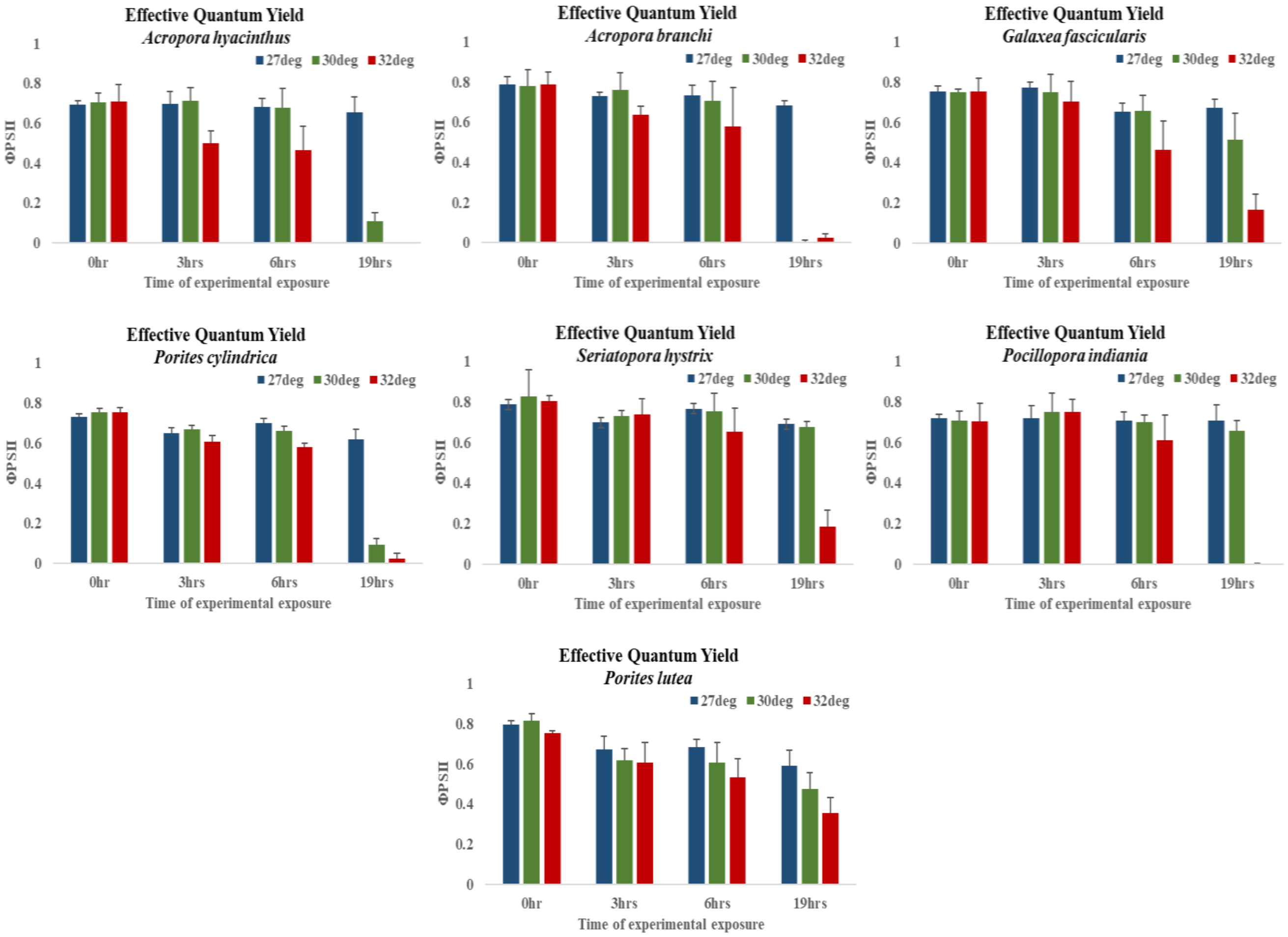
Effective Quantum Yield
Acropora hyacinthus
Effective Quantum Yield
Acropora branchi
Effective Quantum Yield
Galaxea fascicularis
Effective Quantum Yield
Porites cylindrica
Effective Quantum Yield
Seriatopora hystrix
Effective Quantum Yield
Pocillopora indiania
Effective Quantum Yield
Porites lutea

Figure 4. Effective quantum yield at PSII (ΦPSII) of seven coral species at temperatures 27°C (Control), 30°C and 32°C under experimental conditions. The photosynthetic activities were recorded at beginning ($T_{initial}$) of the experiment, after 3 hours of the experiment (T_{3hrs}), after 6 hours of the experiment (T_{6hrs}) and after 19 hours of exposure (T_{19hrs}). Data represents mean±SD (n=9)

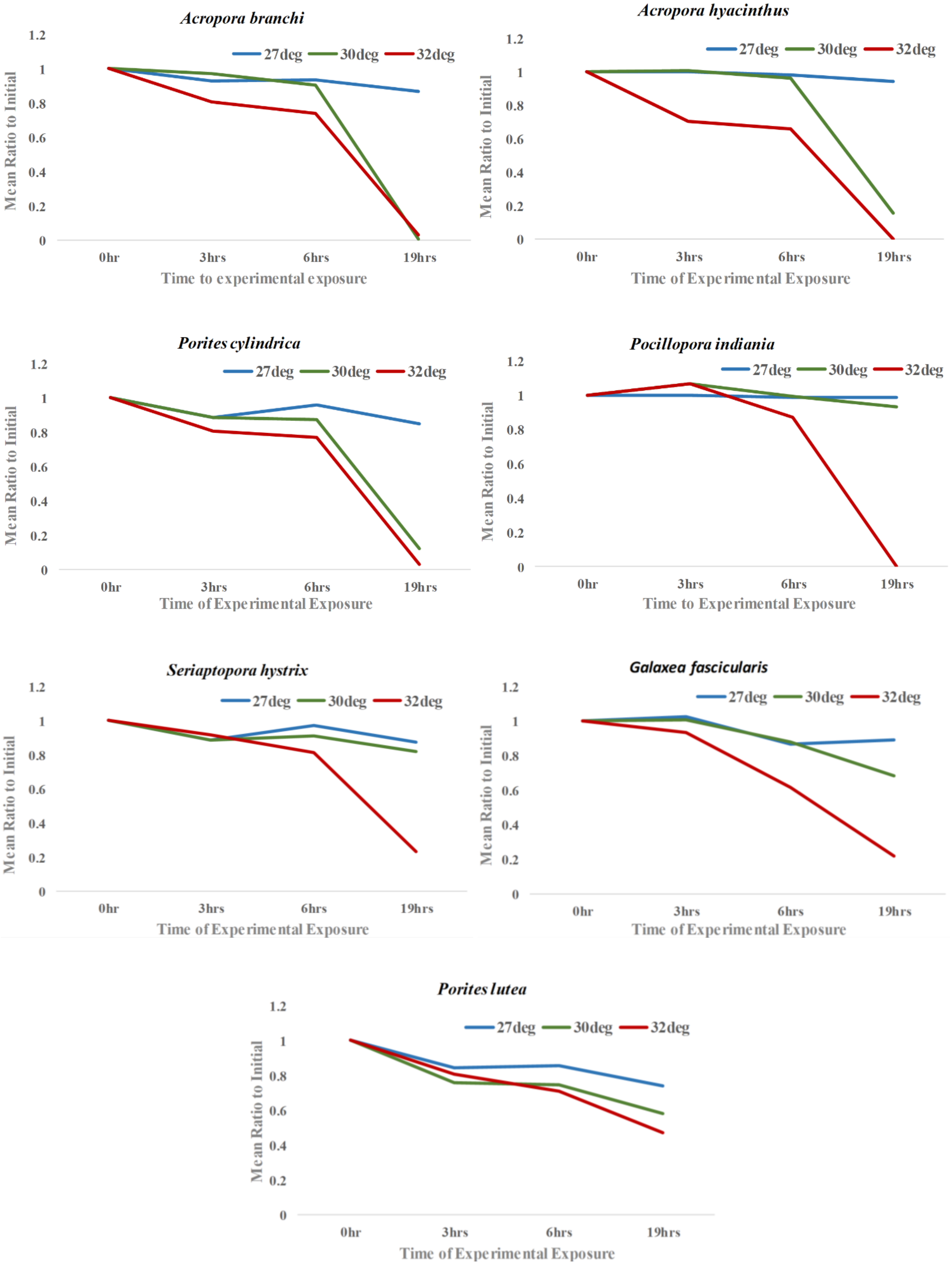

Figure 5. Relative (to T_{0hr}, i.e. initial) effective quantum yield of 7 tested corals exposed to 27°C, 30°C and 32°C over 19hrs

Table 2. Dunn's (1964) Kruskal-Wallis Post-hoc test: Multiple comparison of the mean effective quantum yield (Φ_{PSII}) at different treatments after 3 hours, 6 hours and 19 hours of thermal stress experiment; $p<0.01$, sig. *, $p<0.001$, sig. **, $p<0.0001$, sig. ***

Treatment comparison	3 hours exposure			6 hours exposure			19 hours exposure		
	Z	**p-unadj.**	**p-adj.**	**Z**	**p-unadj.**	**p-adj.**	**Z**	**p-unadj.**	**p-adj.**
27°C - 30°C	-0.408	0.683	0.683	1.116	0.265	0.266	3.284	0.001	0.001
27°C - 32°C	2.101	0.036	0.071	5.224	<0.0001	<0.0001	6.051	<0.0001	<0.0001
30°C - 32°C	2.509	0.012	0.036	4.109	<0.0001	<0.0001	2.766	<0.0001	<0.0001

Discussion

This laboratory-based study established the thermal threshold of two understudied regionally endemic corals, *A. branchi* and *P. indiania,* along with five other morphologically different corals. Overall, the corals displayed a varying degree of thermal tolerances concerning persistent exposures (19 hours) to thermal stresses at 30 and 32°C. Furthermore, it was found that tabular *A. branchi*, *A. hyacinthus* and branching *P. cylindrica* were the most susceptible to bleach and die after 6 hours of exposure to a persistent warmer environment. On the other hand, *P. lutea*, *G. fascicularis, S. hystrix* and *P. indiania* exhibited relatively higher thermal tolerance and these observations concurred with the findings made by van Woesik et al. (2011), Mattan-Moorgawa et al. (2012), Swain et al. (2016) and Cheal et al. (2017). Also, previous studies have demonstrated that tabular Acropora displayed signs of highest level of thermal stresses (Eriksson et al. 2012; Muko et al. 2013) while branching *Acropora* spp. and *Stylophora* spp. (Fitt et al. 2009) were considered more susceptible to bleaching and were the first to bleach and die compared to massive and encrusting corals such as *Porites* spp., *Leptastrea* spp., and *Goniastrea* spp. (Loya et al. 2001; Starko et al. 2023).

Only after three hours of exposure to 32°C, signs of thermal stresses were observed in *A. branchi, A. hyacinthus* and *P. cylindrica* fragments which were expressed by partial bleaching or paling of the coral fragments. Within six hours, the paling further intensified, increasing turbidity due to excessive mucus secretion compared to the 27°C treatments. All the treatments at 32°C had mucus but which varied considerably depending on the species of the coral fragments. Even the treatments containing the fragments of *P. lutea*, *G. fascicularis*, *S. hystrix* and *P. indiania* had accumulated mucus however, it was visibly lower in concentration. In this line, mucus usually acts as a primary defensive mechanism against microbial invasion (Ritchie 2006; Walters et al. 2020) as well as control their microbiome (Walters et al. 2020). Nonetheless, it has also been suggested that during thermal stress, nearly 45% of the total energy budget is concentrated in mucus production, which might be physiologically advantageous for thermally resistant corals as compared to the vulnerable ones as a consequence of further disadvantageously compromising the coral health (Fitt et al. 2009; Zaneveld et al. 2016). Studies have also demonstrated that thermal stresses may cause a reduction in the coral defense mechanism (Vidal-Dupiol et al. 2014; Beatty et al. 2019), while in-depth study on Acroporids revealed that coral immunity is also dependent on the reef health status, whereby the dominant algal reef has a higher risk of coral diseases due to pathogenic bacterial accumulation (Sandin et al. 2008; Louis et al. 2020; Beatty et al. 2022). As such, experimentally, it may be determined that one of the reasons for low thermal resilience in *A. branchi*, *A. hyacinthus* and *P. cylindrica* might have been excessive mucus secretion.

As expected, P. lutea exhibited higher thermal resistance than *G. fascicularis* and *S. hystrix* by actively demonstrating photo-physiological processes to persistent exposure to 32°C. The slow-growing, massive *P. lutea* is among the most studied massive coral and is well known for its thermotolerance (Hoogenboom et al. 2017; Hughes et al. 2018) compared to *G. fascularis* and *S. hystrix*. Despite being previously listed as thermally vulnerable (Loya et al. 2001), under the current laboratory conditions, *G. fascularis* and *S. hystrix* have shown certain level of thermal resistance most potentially owing to enhanced bleaching resilience strategies over repeated heating events (Hoey et al. 2016; Epstein et al. 2022). Given the fact that this study focused mainly on photo-physiological observations, the prediction of precise conditions favoring such thermotolerance was limited, nevertheless, such thermal adaptation may be associated primarily to the high diversity and reef complexity with low water residence time at Riviere des Galets (pers. observation), the sampling site for *G. fascicularis*. For example, certain corals are now capable of withstanding elevated temperatures (>2°C) provided that they have enhanced resilience through dynamic host-symbiont communities (Ziegler et al. 2018) by reshuffling of Symbiodiniaceae (Bhagooli and Hidaka 2003; Fitt et al. 2009; Guest et al. 2012) heterotrophy (Grotolli et al. 2006), shade from algal assemblages giving rise to photo acclimatization most potentially in the case of *S. hystrix* (Lewis et al. 2022) which are essential adaptive criteria for local thermal resistance and acclimatization.

So far, despite being limited to the assessment to only photosynthetic activities of morphologically different corals, this study has been able to assess the thermal threshold of the understudied *A. branchi* and *P. indiania*, the regionally endemic corals of the Western Indian Ocean region. Additionally, the degree of thermal vulnerability of *A. hyacinthus* and the thermal resistance of *P. lutea* was confirmed whereas the unexpectedly enhanced thermal tolerance of *S. hystrix* and *G. fascicularis* was detected. This experiment provided a preliminary insight on the potential thermal tolerance in some corals of Mauritius and has shown that these corals might have strategized to enhance their thermo-resilience (Mattan-Moorgawa et al. 2020) while others in the like of tabular and branching ones are still struggling to withstand thermal stresses (Hoey et al. 2016). Also, such findings on thermal resilience of regionally endemic and morphologically different coral species are essential for onwards reef conservation and also for the selection of robust coral species for reef restoration. Nevertheless, in-depth evaluation through additional experimental parameters on these corals, such as the maximum Electron Transport Rate (ETRmax), Non-Photochemical Quenching (NPQ), study on heterotrophic feeding, microbiomes and Symbiodiniaceae community structure, is critical to providing science-driven information on photoacclimation and photoprotection on the reefs of the Western Indian Ocean region to better strategize on innovative conservation measures.

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REFERENCES

Baird AH, Marshall PA. 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 237: 133-141. DOI: 10.3354/meps237133.

Beatty DS, Clements CS, Valayil JM, Jarvis SY, Ritchie KB, Stewart FJ, Hay ME. 2022. Variance of coral anti-pathogen defense in response to transplantation between coral-and macroalgal-dominated reefs. Coral Reefs 41 (5): 1417-1431. DOI: 10.1007/s00338-022-02291-2.

Beatty DS, Valayil JM, Clements CS, Ritchie KB, Stewart FJ, Hay ME. 2019. Variable effects of local management on coral defenses against a thermally regulated bleaching pathogen. Sci Adv 5 (10): eaay1048. DOI: 10.1126/sciadv.aay1048.

Bhagooli R, Hidaka M. 2003. Comparison of stress susceptibility of *in hospite* and isolated zooxanthellae among five coral species. J Exp Mar Biol Ecol 291: 181-197. DOI: 10.1016/s0022-0981(03)00121-7.

Bhagooli R, Kaullysing D. 2019. Seas of Mauritius. World Seas: An Environmental Evaluation. Elsevier, Amsterdam. DOI: 10.1016/b978-0-08-100853-9.00016-6.

Bhagooli R, Mattan-Moorgawa S, Kaullysing D, Chumun PK, Klaus R, Munbodhe V. 2021a. Status and sustainability of reefs and shorelines of the Republic of Mauritius. In: Gunputh RP (Eds). Sustainable Development Goals. Star Publications Pvt. Ltd., New Delhi, India.

Bhagooli R, Mattan-Moorgawa S, Kaullysing D, Louis YD, Gopeechund A, Ramah S, Soondur M, Pilly SS, Beesoo R, Wijayanti DP, Bachok ZB, Monrás VC, Casareto BE, Suzuki Y, Baker AC. 2021b. Chlorophyll fluorescence-A tool to assess photosynthetic performance and stress photophysiology in symbiotic marine invertebrates and seaplants. Mar Pollut Bull 165: 112059. DOI: 10.1016/j.marpolbul.2021.112059.

Bhagooli R, Sheppard CRC. 2012. Prediction of recurrences of mass coral bleaching/mortality and vulnerability of reef-building corals to climate change in Mauritian and Japanese waters. Univ Mauritius Res J Spec Issue: Sustain Mar Environ 18: 105-121.

Bhagooli R, Soondur M, Ramah S, Gopeechund A, Jeetun S, Kaullysing D. 2021c. Photo-physiology of healthy and bleached corals from the Mascarene Plateau. Special Issues 2/2021-Studies on the Mascarene Plateau. West Indian Ocean J Mar Sci 2: 109-120. DOI: 10.4314/wiojms.si2021.2.8.

Bhagooli R, Taleb-Hossenkhan N. 2012. Thermal spatial heterogeneity and coral bleaching: Implications for habitat refuges. Proc 12th Inter Coral Reef Symp, 9D Refuges for corals in time and space.

Borell EM, Bischof K. 2008. Feeding sustains photosynthetic quantum yield of a scleractinian coral during thermal stress. Oecologia 157 (4): 593-601. DOI: 10.1007/s00442-008-1102-2.

Cheal AJ, MacNeil MA, Emslie MJ, Sweatman H. 2017. The threat to coral reefs from more intense cyclones under climate change. Glob Chang Biol 23 (4):1511-1524. DOI: 10.1111/gcb.13593.

Daby D. 2006. Current patterns and the distribution of benthic habitats in a coastal lagoon of Mauritius. Hydrobiologia 556: 47-60. DOI: 10.1007/s10750-005-0593-7.

Elliott JA, Patterson MR, Staub CG, Koonjul M, Elliott SM. 2018. Decline in coral cover and flattening of the reefs around Mauritius (1998-2010). PeerJ 6 (11): e6014. DOI: DOI: 10.7717/peerj.6014.

Fai ALY, Kaullysing D, Jeetun S, Soondur M, Bhagooli R. 2023. *Diplosoma simile* (Ascidiacea: Didemnidae) distribution and its photosynthetic thermal stress responses from Mauritius: Implications for invasive or opportunistic behavior. Indo Pac J Ocean Life 7 (1): 16-26. DOI: 10.13057/oceanlife/o070102.

Fitt WK, Gates RD, Hoegh-Guldberg O, Bythell JC, Jatkar A, Grottoli AG, Gomez M, Fisher P, Lajeunesse TC, Pantos O, Iglesias-Prieto R, Franklin DJ, Rodrigues LJ, Torregiani JM, van Woesik R, Lesser MP. 2009. Response of two species of Indo-Pacific corals, *Porites cylindrica* and *Stylophora pistillata*, to short-term thermal stress: The host does matter in determining the tolerance of corals to bleaching. J Exp Mar Biol Ecol 373: 102-110. DOI: 10.1016/j.jembe.2009.03.011.

Fujise L, Yamashita H, Suzuki G, Sasaki K, Liao LM, Koike K. 2014. Moderate thermal stress causes active and immediate expulsion of photosynthetically damaged zooxanthellae (*Symbiodinium*) from corals. PloS One 9: e114321. DOI: 10.1371/journal.pone.0114321.

Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD, Schoepf V, McGinley M, Baumann J, Matsui Y. 2014. Cumulative impact of annual coral bleaching can turn some coral species winners into losers. Glob Chang Biol 12: 3823-3833. DOI: 10.1111/gcb.12658.

Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver EC, Benthuysen JA, Burrows MT, Donat MG, Feng M, Holbrook NJ. 2016. A hierarchical approach to defining marine heatwaves. Prog Oceanogr 141: 227-238. DOI: 10.1016/ j.pocean.2015.12.014.

Hoey AS, Howells E, Johansen JL, Hobbs JPA, Messmer V, McCowan DM, Wilson SK, Pratchett MS. 2016. Recent advances in understanding the effects of climate change on coral reefs. Diversity 8 (2): 12. DOI: 10.3390/d8020012.

Holbrook SJ, Adam TC, Edmunds PJ, Schmitt RJ, Carpenter RC, Brooks AJ, Lenihan HS, Briggs CJ. 2018. Recruitment drives spatial variation in recovery rates ofresilient coral reefs. Sci Rep 8: 7338. DOI: 10.1038/s41598-018-25414-8.

Hoogenboom MO, Campbell DA, Beraud E, Dezeeuw K, Ferrier-Pages C. 2012. Effects of light, food availability and temperature stress on the function of photosystem II and photosystem I of coral symbionts. PLoS One 7 (1): e30167. DOI: 10.1371/journal.pone.0030167.

Hoogenboom MO, Frank GE, Chase TJ, Jurriaans S, Álvarez-Noriega M, Peterson K, Critchell K, Berry KLE, Nicolet KJ, Ramsby B, Paley AS. 2017. Environmental drivers of variation in bleaching severity of *Acropora* species during an extreme thermal anomaly. Front Mar Sci 4: 376. DOI: 10.3389/fmars.2017.00376.

Hughes TP, Anderson KD, Connolly SR et al. 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359 (6371): 80-83. DOI: 10.1126/science.aan8048.

Hughes TP, Kerry JT, Álvarez-Noriega M et al. 2017. Global warming and recurrent mass bleaching of corals. Nature 543: 373-377. DOI: 10.1038/nature21707.

Jeetun S, Ricot M, Taleb-Hossenkhan N, Kaullysing D, Flot JF, Bhagooli R. 2023. Differential responses of effective quantum yield to acute thermal stress in scleractinian corals including pre- and post-transplanted *Acropora muricata*. Indo Pac J Ocean Life 7 (1): 54-63. DOI: 10.13057/oceanlife/o060106.

Klepac CN, Barshis DJ. 2022. High-resolution in situ thermal metrics coupled with acute heat stress experiments reveal differential coral bleaching susceptibility. Coral Reefs 41: 1045-1057. DOI: 10.1007/s00338-022-02276-1.

Lewis BM, Suggett DS, Prentis PJ, Nothdurft LD. 2022. Cellular adaptations leading to coral fragment attachment on artificial substrates in *Acropora millepora* (Am-CAM). Sci Rep 12 (1): 1-18. DOI: 10.1038/s41598-022-23134-8.

Lough JM, Anderson KD, Hughes TP. 2018. Increasing thermal stress for tropical coral reefs: 1871-2017. Sci Rep 8 (1): 1-8. DOI: 10.1038/s41598-018-24530-9.

Louis YD, Bhagooli R, Seveso D, Maggioni D, Galli P, Vai M, Dyall SD. 2020. Local acclimatisation-driven differential gene and protein expression patterns of Hsp70 in *Acropora muricata*: Implications for coral tolerance to bleaching. Mol Ecol 29 (22): 4382-4394. DOI: 10.1111/mec.15642.

Louis YD, Kaullysing D, Gopeechund A, Mattan-Moorgawa S, Bahorun T, Dyall SD, Bhagooli R. 2016. *In hospite Symbiodinium* photophysiology and antioxidant responses in *Acropora muricata* on a coast-reef scale: Implications for variable bleaching patterns. Symbiosis 68: 61-72. DOI: 10.1007/s13199-016-0380-4.

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R. 2001. Coral bleaching: The winners and the losers. Ecol Lett 4 (2): 122-131. DOI: 10.1046/j.1461-0248.2001.00203.x.

Mattan-Moorgawa S, Bhagooli R, Rughooputh SDDV. 2012. Thermal stress physiology and mortality responses in scleractinian corals of Mauritius. In Proceedings of the 12th International Coral Reef Symposium. Cairns, Australia.

Mattan-Moorgawa S, Chumun PK, Taleb-Hossenkhan N, Rughooputh SDDV, Bhagooli R. 2020. Variable thermal and biochemical stress responses of tissue balls from *Lithophyllon repanda*, *Pocillopora damicornis* and *Acropora muricata*. Galaxea, J Coral Reef Stud 22 (1): 37-50. DOI: 10.3755/galaxea.22.1_37.

McClanahan T, Munbodhe V, Naggea J, Muthiga N, Bhagooli, R. 2021. Rare coral and reef fish species status, possible extinctions, and associated environmental perceptions in Mauritius. Conserv Sci Prac 3 (11): e527. DOI: 10.1111/csp2.527.

McClanahan TR, Muthiga NA. 2020. Change in fish and benthic communities in Belizean patch reefs in and outside of a marine reserve, across a parrotfish capture ban. Mar Ecol Prog Ser 645: 25-40. DOI: 10.3354/meps13357.

McWilliam JN, McCauley RD, Erbe C, Parsons MJG. 2018. Soundscape diversity in the Great Barrier Reef: Lizard Island, a case study. Bioacoustics 27: 295-311. DOI: 10.1080/09524622.2017.1344930.

Muko S, Arakaki S, Nagao M, Sakai K. 2013. Growth form-dependent response to physical disturbance and thermal stress in *Acropora* corals. Coral Reefs 32: 269-280. DOI: 10.1007/s00338-012-0967-z.

Obura DO, Aeby G, Amornthammarong N et al. 2019. Coral reef monitoring, reef assessment technologies, and ecosystem-based management. Front Mar Sci 6: 580. DOI: 10.3389/fmars.2019.00580.

Obura DO, Gudka M, Rabi FA, Gian SB, Bijoux J, Freed S, Maharavo J, Mwaura J, Porter S, Sola E, Wickel J, Yahya S, Ahamada S. 2017. Coral reef status report for the Western Indian Ocean. Global Coral Reef Monitoring Network (GCRMN)/International Coral Reef Initiative (ICRI), Nairobi convention, Kenya.

Obura DO. 2012. The diversity and biogeography of Western Indian Ocean reef-building corals. PLoS One 7(9): e45013. DOI: 10.1371/journal.pone.0045013.

Richardson LE, Graham NAJ, Pratchett MS, Eurich JG, Hoey AS. 2018. Mass coral bleaching causes biotic homogenization of reef fish assemblages. Glob Chang Biol 24 (7): 3117-3129. DOI: 10.1111/gcb.14119.

Ricot M, Jeetun S, Jogee SY, Kaullysing D, Taleb-Hossenkhan N, Bhagooli R. 2023. Thermal photo-physiological responses of massive heat-resistant coral *Porites lutea* under fish predated versus non-predated conditions. Indo Pac J Ocean Life 7 (1): 38-47. DOI: 10.13057/oceanlife/o070104.

Ritchie KB. 2006. Regulation of microbial populations by coral surface mucus and mucus-associated bacteria. Mar Ecol Prog Ser 322: 1-14. DOI: 10.3354/meps322001.

Safaie A, Silbiger NJ, McClanahan TR, Pawlak G, Barshis DJ, Hench JL, Rogers JS, Williams GJ, Davis KA. 2018. High frequency temperature variability reduces the risk of coral bleaching. Nat Commun 9 (1): 1671. DOI: 10.1038/s41467-018-04074-2.

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E. 2008. Baselines and degradation of coral reefs in the Northern Line Islands. PloS One 3 (2): e1548. DOI: 10.1371/journal.pone.0001548.

Serrano XM, Miller MW, Hendee JC, Jensen BA, Gapayao JZ, Pasparakis C, Grosell M, Baker AC. 2018. Effects of thermal stress and nitrate enrichment on the larval performance of two Caribbean reef corals. Coral Reefs 37: 173-182. DOI: 10.1007/s00338-017-1645-y.

Shantz AA, Burkepile DE. 2014. Context-dependent effects of nutrient loading on the coral-algal mutualism. Ecology 95 (7): 1995-2005. DOI: 10.1890/13-1407.1.

Starko S, Fifer J, Claar DC, Davies SW, Cunning R, Baker AC, Baum JK. 2023. Marine heatwaves threaten cryptic coral diversity and erode associations amongst coevolving partners. bioRxiv 2023: 1-35. DOI: 10.1101/2023.01.07.522953.

Steffen W, Burbidge A, Hughes L, Kitching R, Lindenmayer D, Musgrave W, Smith MS, Werner P. 2009. Australia's Biodiversity and Climate Change. CSIRO Publishing, Clayton.

Stillman JH. 2019. Heat waves, the new normal: Summertime temperature extremes will impact animals, ecosystems, and human communities. Physiology 34: 86-100. DOI: 10.1152/physiol.00040.2018.

Swain TD, DuBois E, Gomes A, et al. 2016. Skeletal light-scattering accelerates bleaching response in reef-building corals. BMC Ecol 16 (1): 1-18. DOI: 10.1186/s12898-016-0061-4.

Tebbett SB, Connolly SR. Bellwood DR. 2023. Benthic composition changes on coral reefs at global scales. Nat Ecol Evol 7 (1): 71-81. DOI: 10.1038/s41559-022-01937-2.

Tilstra A, Bednarz VN, Cardini U, van Hoytema N, Al-Rshaidat MM, Wild C. 2017. Seasonality affects dinitrogen fixation associated with two common macroalgae from a coral reef in the northern Red Sea. Mar Ecol Prog Ser 575: 69-80. DOI: 10.3354/meps12206.

van Hooidonk R, Maynard J, Tamelander J, Gove J, Ahmadia G, Raymundo L, Williams G, Heron SF, Planes S. 2016. Local-scale projections of coral reef futures and implications of the Paris Agreement. Sci Rep 6 (1): 39666. DOI: 10.1038/srep39666.

van Woesik R, Sakai K, Ganase A, Loya Y. 2011. Revisiting the winners and the losers a decade after coral bleaching. Mar Ecol Prog Ser 434: 67-76. DOI: 10.3354/meps09203.

Vidal-Dupiol J, Dheilly NM, Rondon R, Grunau C, Cosseau C, Smith KM, Freitag M, Adjeroud M, Mitta G. 2014. Thermal stress triggers broad *Pocillopora damicornis* transcriptomic remodeling, while *Vibrio coralliilyticus* infection induces a more targeted immuno-suppression response. PloS One 9 (9): e107672. DOI: 10.1371/journal.pone.0107672.

Voolstra CR, Buitrago-López C, Perna G, Cárdenas A, Hume BCC, Rädecker N, Barshis DJ. 2020. Standardized short-term acute heat stress assays resolve historical differences in coral thermotolerance across microhabitat reef sites. Glob Chang Biol 26 (8): 4328-4343. DOI: 10.1111/gcb.15148.

Walters BM, Connelly MT, Young B, Traylor-Knowles N. 2020. The complicated evolutionary diversification of the Mpeg-1/Perforin-2 family in Cnidarians. Front Immunol 11: 1690. DOI: 10.3389/fimmu.2020.01690.

Zaneveld JR, Burkepile DE, Shantz AA, Pritchard CE, McMinds R, Payet JP, Welsh R, Correa AMS, Lemoine NP, Rosales S, Fuchs C, Maynard JA, Thurber RV. 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nat Commun 7: 11833. DOI: 10.1038/ncomms11833.

Ziegler M, Eguíluz VM, Duarte CM, Voolstra CR. 2018. Rare symbionts may contribute to the resilience of coral-algal assemblages. ISME J 12 (1): 161-172. DOI: 10.1038/ismej.2017.151.